Plant growth and respiration re-visited: maintenance respiration defined – it is an emergent property of, not a separate process within, the system – and why the respiration : photosynthesis ratio is conservative

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• *Background and Aims* Plant growth and respiration still has unresolved issues, examined here using a model. The aims of this work are to compare the model's predictions with McCree's observation-based respiration equation which led to the 'growth respiration/maintenance respiration paradigm' (GMRP) – this is required to give the model credibility; to clarify the nature of maintenance respiration (MR) using a model which does not represent MR explicitly; and to examine algebraic and numerical predictions for the respiration: photosynthesis ratio.
• *Methods* A two-state variable growth model is constructed, with structure and substrate, applicable on plant to ecosystem scales. Four processes are represented: photosynthesis, growth with growth respiration (GR), senescence giving a flux towards litter, and a recycling of some of this flux. There are four significant parameters: growth efficiency, rate constants for substrate utilization and structure senescence, and fraction of structure returned to the substrate pool.
• *Key Results* The model can simulate McCree's data on respiration, providing an alternative interpretation to the GMRP. The model's parameters are related to parameters used in this paradigm. MR is defined and calculated in terms of the model's parameters in two ways: first during exponential growth at zero growth rate; and secondly at equilibrium. The approaches concur. The equilibrium respiration:photosynthesis ratio has the value of 0·4, depending only on growth efficiency and recycling fraction.
• *Conclusions* McCree's equation is an approximation that the model can describe; it is mistaken to interpret his second coefficient as a maintenance requirement. An MR rate is defined and extracted algebraically from the model. MR as a specific process is not required and may be replaced with an approach from which an MR rate emerges. The model suggests that the respiration:photosynthesis ratio is conservative because it depends on two parameters only whose values are likely to be similar across ecosystems.

Key words: Respiration, growth, maintenance, model, senescence, recycling, photosynthesis, gross production, net production, respiration:photosynthesis ratio.

INTRODUCTION

There continues to be considerable discussion of respiration. This is focused partly on how to handle maintenance respiration (MR) when working within the 'growth respiration/maintenance respiration paradigm' (GMRP) (Amthor, 2000) and partly on the ratio (r) of respiration (R) to gross photosynthesis (P_g) in plant ecosystems, defined as $r_{R:P_g}$. There is concern as to whether $r_{R:P_g}$ is constant or variable. The topic is important in addressing some climate change issues, such as short-term and long-term contributions of plant ecosystems to carbon (C) sequestration. On one hand are simplifying and perhaps optimistic holists, who would like to assume that $r_{R:P_g}$ is approximately constant over a range of species and conditions (e.g. Gifford, 2003). This might permit construction of simple ecosystem models applicable to climate problems. A recent example of this is Van Oijen *et al.* (2010), who, working within GMRP, with some assumptions, demonstrate that a more or less constant value of the ratio is

to be expected, partly as a result of conservation of matter (stoichiometry). On the other are reductionists who might also consider themselves as realists. The latter, to which group I mostly adhere, make efforts to understand the detailed mechanisms of respiration which cause $r_{R:P_g}$ to fall below unity and, possibly, be rather variable (Cannell and Thornley, 2000; Thornley and Cannell, 2000). Amthor (2000) gives an excellent review of plant respiration, supplying a valuable historical perspective and also the current state of the art – there have been no substantive advances in the past decade.

Maintenance respiration is often considered to be a distinct portion of respiration, but it has long been regarded sceptically. Wohl and James (1942), remarked that 'It is a facile assumption that the energy change revealed by the continuous liberation of heat from mature tissues which are neither doing external work nor synthesizing appreciably, is a measure of the energy of maintenance. The assumption will not stand closer inspection . . .'.

The construction and analysis of simple models can sometimes be employed to illuminate important problems; this is

what is attempted below. A simple model without a mainten-ance component is described. Solutions are obtained, focusing on two important phases in the growth dynamics: exponential growth and the steady state. The first phase, exponential growth, is transient, but it often lasts sufficiently long to be characterizable, and it is amenable to experimentation. The second phase, the steady state, is important because many plant ecosystems may be approximately in a steady state, although it can be less accessible to experimentation.

We define the specific MR rate (ρ_m; d^{-1}) as being the specific respiration rate when the growth rate is zero, i.e. when the *status quo* is maintained. The growth rate can be zero in two cases: when the plant is in the exponential growth (eg) phase but is growing at zero rate; and when the plant is in the steady state (ss) (its mass has reached an asymptote). In both cases, the same expression is obtained for the specific MR rate, depending on three parameters of the model (Fig. 1). This permits a re-parameterization of the model, which can, with assumptions, be simplified to a form perhaps more acceptable to the holists.

Current understanding of plant respiration was given impetus and direction by the findings of McCree (1970), and his famous equation:

$$R = kP + cW \qquad (1)$$

where R is 24 h respiration (kg CO_2 m^{-2} d^{-1}), P is daily gross photosynthesis (kg CO_2 m^{-2} d^{-1}), W is plant mass (kg CO_2 equivalents), k is a constant (dimensionless), and c is has units of d^{-1}. McCree applied a 12 h light period during a 24 h day. Details of how R and P are obtained from the measurements are given by McCree (1970), a procedure which could be affected by daylength. McCree's estimate of the parameters was $k = 0.25$ and $c = 0.015$ d^{-1}. Dividing through by dry mass W gives

$$\frac{R}{W} = k\frac{P}{W} + c = 0.25\frac{P}{W} + 0.015 \qquad (2)$$

This equation relates a specific 24 h respiration rate to a specific daily gross photosynthetic rate. The simplicity and intuitiveness of these equations has contributed greatly to the appeal of the GMRP paradigm, with c being interpreted as a maintenance coefficient.

The situation here may be compared with micro-organisms in a chemostat (Pirt, 1965), where it is possible, in a true steady state without diurnality, to measure directly the gross rate of supply of substrate, respiration rate and also growth rate. This leads to a similar equation.

The meaning of eqns (1) and (2) has been much discussed over the years (Amthor, 2000). A common interpretation is that respiration is viewed as having two components: one results from growth of the organism [growth respiration (GR)]; the other (MR) is attributed to the organism maintaining its *status quo* (Pirt, 1965; Thornley, 1970).

Two objections can be raised against GMRP. The first is on scientific grounds: the biochemical and other processes occur-ring in a growing organism are qualitatively the same as those which occur in an organism which is maintaining the *status quo*. This especially applies to the metabolic processes which give rise to respiration and yield ATP and reducing power, but also those anabolic processes which are synthesiz-ing compounds which in some cases are replacing compounds that have recently been catabolized. In general, there is not a distinct set of processes which can be said to belong to 'main-tenance', and another set which belongs to 'growth', although catabolic processes (such as protein breakdown) may lead to a growth-associated process (protein synthesis) maintaining the *status quo* of the plant and giving a respiratory flux which can be dubbed maintenance.

The second objection is a practical matter: many authors have used the paradigm when constructing models of plant growth, crop growth and plant ecosystems. Again and again unaccepta-ble behaviour of the model has occurred, and the maintenance component has to be arbitrarily 'fixed'. For example, de Wit *et al.* (1970, p. 61) remarked 'Simulation of this viewpoint leads to inconsistent results. If it is assumed that the respiration per unit plant material is low, it appears that yield levels which are observed in the field may be obtained, but then simulated res-piration rates under controlled conditions are far too small. If it is assumed that respiration per unit of plant material is higher, simulated respiration rates under controlled conditions may be in the observed range, but then simulated ceiling yields in the field are far too small.' Loomis (1970, p. 140, 141) states 'The McCree equation $R = kP + cW$ summarizes well certain data … but it would be a mistake to assume it holds *a priori* for other situations, …', and 'The big difficulty is, of course, in accounting for 'maintenance' respiration …'. The impasse is
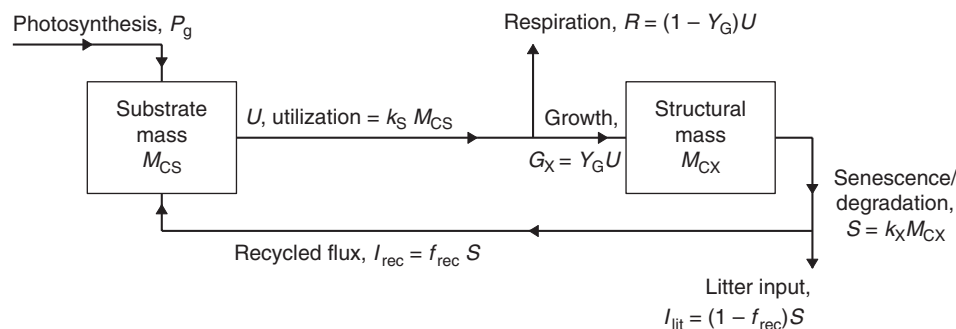

FIG. 1. Plant growth model for respiration. The two state variables are substrate mass, M_{CS}, and structural mass, M_{CX}. There are four key parameters: Y_G, growth efficiency – fraction of substrate C utilized for growth which appears in structure – the remaining fraction $(1 - Y_G)$ is respired; f_{rec}, fraction of senescing/degrading structural C recycled to substrate, the remainder becoming litter; k_S, rate constant for substrate utilization; and k_X senescence rate constant.

resolved (typically) by making the maintenance coefficient variable, e.g. Seginer (2003) assumes that the maintenance coefficient depends asymptotically on plant structural mass. Van Oijen *et al.* (2010) assume that MR equals GR, an assumption tantamount to jettisoning GMRP in favour of a growth-only respiration model. Others assume that the MR rate coefficient depends on the availability of substrates (e.g. Thornley, 1998, p. 38), as in the growth process. The problems revolve around issues such as: a common substrate (carbohydrate) is used for both growth and maintenance; priorities (more explicitly, utilization rate constants) have to be assigned between growth and maintenance; and these priorities need to change according to substrate supply and utilization (which determine substrate fraction). There is no straightforward way of dealing with growth and maintenance separately because the pools and anabolic processes are the same for both growth and maintenance. Many modellers do not like to represent substrates because their representation is perceived to be difficult (which it can be), although consideration of the differences between sub-arctic and semi-tropical plant ecosystems, and the diurnality of many plant variables including substrate pools might suggest that their representation is essential for realism.

Here a two-state variable model (structure and substrate; Warren Wilson, 1967) is described. 'Substrate' includes storage (easily remobilizable) components. The model is a simplification and extension of a model proposed some years ago (Thornley, 1977; see also Loehle, 1982, who expanded on the 1977 model and provided a reconciliation of it with the more traditional view of respiration). The simplification is that non-degradable structure is omitted so that steady-state solutions can be derived, providing the insights that can be obtained from analytical expressions. The extension is that senescence is included, again so that steady-state solutions can be obtained. The significant processes are photosynthesis, growth with GR, senescence and recycling to the substrate pool. Respiration is an output of the growth process alone. Maintenance is not a feature. The model is simple enough (with three significant constants) to permit a thorough exploration of its properties, for both exponential growth and the steady state. My first objective is to demonstrate that its predictions are reasonably compatible with McCree's equation [our eqn (1)] (McCree, 1970), and therefore provides an alternative to the GMRP. My second objective is to define and extract a specific MR rate for a non-growing plant (which can occur in two ways). My last objective is to show that the model gives explicit expressions and acceptable and conservative predictions for the respiration:photosynthesis ratio ($r_{R:P_g}$), which for plant ecosystems is often in the range 0·4–0·5. Approximate expressions for the parameters of McCree's equation can be derived in terms of the significant parameters of the current model.

MODEL AND METHODS

The scheme is drawn in Fig. 1. Variables and parameters are listed in Table 1. The two state variables (pools) are M_{CS} (kg substrate C m^{-2}) and M_{CX} (kg structural C m^{-2}); these are per unit ground area. Next the fluxes in Fig. 1 are calculated, all having units of kg C m^{-2} (ground) d^{-1}.

Photosynthesis, P$_g$

The expression used for gross photosynthesis [eqn (4)] has a long pedigree, and is parameterized with familiar quantities. It gives the correct dependencies on plant size (leaf area index), light flux density, photosynthetic efficiency and light-saturated leaf photosynthesis. These are needed because we shall be comparing our results with measured data.

First calculate the leaf area index, L_{AI}, from structural mass, M_{CX}, with

$$L_{AI} = L_{AR}M_{CX}. \quad L_{AR} = 50 \, \text{m}^2 \, \text{leaf (kg structural C)}^{-1} \quad (3)$$

Leaf area ratio, L_{AR}, is a rounded value obtained from Causton and Venus (1981, p. 46, fig. 2·6a) who give a leaf area ratio of about 0·02 m^2 (g total mass)$^{-1}$. Note that L_{AR} is a 'structural' leaf area ratio, with reference to just the structural biomass C component. Therefore, it is higher than usual, which is per unit of total biomass. We assumed that 40 % of total dry mass is structural C (50 = 1000 × 0·02/0·4). It is assumed that L_{AR} is constant in order to make a simple analysis feasible. However, Bertin and Gary (1998) examined leaf mass per area (LMA, g m^{-2}) in tomato, manipulating light, CO_2 and fruit load. They found substantial variations of incremental LMA related to source/sink status and sugar and starch content, and used their findings to modify their modelling of tomato plant growth. Such modelling requires keeping track of leaf area age distribution and increases complexity greatly (e.g. Thornley, 1998, pp. 48–49).

Gross photosynthetic rate, P_g (kg C m^{-2} d^{-1}), is calculated with

$$P_g = \frac{12}{44}86400[1 - \exp(-L_{AI})]\frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}}$$
$$= \frac{12}{44}86400[1 - \exp(-L_{AR}M_{CX})]\frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}}$$
$$\alpha = 1 \cdot 0 \times 10^{-8} \, \text{kg} \, CO_2 (\text{J PAR})^{-1} \equiv 0 \cdot 05 \, \text{mol} \, CO_2$$
$$(\text{quantum PAR})^{-1}$$
$$I_0 = 50 \, \text{J (PAR) m}^{-2} \, \text{s}^{-1} \equiv 230 \, \mu\text{mol PAR m}^{-2} \, \text{s}^{-1}$$
$$P_{max} = 0 \cdot 5 \times 10^{-6} \, \text{kg} \, CO_2 \, \text{m}^{-2} \, \text{s}^{-1} \equiv 11 \cdot 4 \, \mu\text{mol} \, CO_2 \, \text{m}^{-2} \, \text{s}^{-1}$$
$$(4)$$

P_g is, via eqn (3), a function of the structure state variable, M_{CX}. This equation is based on a continuous canopy of leaf area index L_{AI}, light flux density incident on the top of the canopy of I_0, exponential decrease in light level on descending into the canopy of exp($- L_{AI}$), a rectangular hyperbola for leaf response to light [$P_{leaf} = \alpha I_0 P_{max}/(\alpha I_0 + P_{max})$, kg CO_2 m^{-2} (leaf) s^{-1}] with photosynthetic efficiency of α, a light-saturated photosynthetic rate of P_{max} at the top of the canopy which decreases as exp($-L_{AI}$) on descending in the canopy, and black leaves with a canopy extinction coefficient of unity [see, for example, Thornley and France, 2007, pp. 297–298, equation (9·50) with $k = 1$ and $m = 0$]. The

TABLE 1. *State variables, parameters and definitions: relevant equation numbers are indicated*

(a)

State variable	Description	Initial ($t = 0$) value
M_{CS}	Mass of substrate C [eqns (17), (11)]	0·000005 kg substrate C m^{-2} [= 0·05 M_{CX} ($t = 0$)]
M_{CX}	Mass of structural C [eqns (17)]	0·0001 kg structural C m^{-2}

(b)

Parameter + value	Description	Units [with alternative where applicable]
$f_{dl} = 0.5$	Fractional day length [(43)]	h daylight (24 h)$^{-1}$
$f_{rec} = 0.5$	Fraction of senescence flux recycled [eqns (16), Fig. 1]	
$I_0 = 50$ [230] (continuous light) 100 [460] (12 h day)	Light flux density at top of canopy [eqns (4), (44)]	J (PAR) m^{-2} s^{-1} [μmol (PAR) m^{-2} s^{-1}]
$k_S = 1$	Rate constant for substrate utilization [eqns (12)]	d^{-1}
$k_X = 0.04$	Senescence rate constant [eqns (15)]	d^{-1}
$L_{AR} = 50$	Leaf area ratio [eqns (3)]	m^2 leaf (kg structural C)$^{-1}$
$P_{max} = 0.5 \times 10^{-6}$ [11·4]	Saturating photosynthetic rate at top of canopy [eqns (4)]	kg CO$_2$ m^{-2} s^{-1} [μmol CO$_2$ m^{-2} s^{-1}]
$Y_G = 0.75$	Growth efficiency [eqns (13)]	kg structural C (kg substrate C)$^{-1}$
$\alpha = 10^{-8}$ [0·05]	Photosynthetic efficiency [eqns (4)]	kg CO$_2$ (J PAR)$^{-1}$ [mol CO$_2$ (quantum PAR)$^{-1}$]
$\beta = 0.39$	Constant for linearized gross photosynthetic rate at $I_0 = 100$ [eqns (8)]	kg C substrate (kg structural C)$^{-1}$ d^{-1}
$\rho_m = 0.0127$	Specific maintenance respiration rate [eqns (31), (42)]	d^{-1}

(c)

Variable	Description	Units
C_S, C_S(eg), C_S(ss)	Substrate fraction [eqn (11)], in exponential growth [eqns (25), (27)], in steady state [eqns (42)]	kg substrate C (kg structural C)$^{-1}$
$f_{Rnight:R24h}$	Fraction of 24 h respiration occurring at night [eqns (47)]	
G_X	Structural growth rate (gross) [eqns (13)]	kg structural C m^{-2} d^{-1}
I_{lit}	Litter flux [eqns (16), Fig. 1]	kg C m^{-2} d^{-1}
I_{rec}	Recycled flux to substrate pool [eqns (16), Fig. 1]	kg C m^{-2} d^{-1}
L_{AI}	Leaf area index [eqns (3)]	m^2 leaf (m^2 ground)$^{-1}$
M_C	Total mass of system [eqns (18)]	kg total C m^{-2}
P_g, P_n, P_g(ss), P_n(ss), $P_{g,day}$, $P_{n,day}$	Gross, net photosynthetic rates [eqns (4), (19)]; steady-state values [eqns (36), (38), (41)]; daily values [eqns (45), (47)]	kg C m^{-2} d^{-1}
R, R_{night}, R(ss), R_{24h}	Respiration rate [eqns (13)], night-time integral [eqns (47)], steady-state value [eqns (41)], daily value [eqns (45)]	kg C m^{-2} d^{-1}
$r_{R:P_g}$, $r_{R:P_g}$(eg), $r_{R:P_g}$(ss), $r_{Rnight:Pnday}$, $r_{R24h:Pgday}$	Ratios of: respiration to gross photosynthesis [eqns (21)], in exponential growth [eqn (34)], in steady state [eqns (42)], night respiration to daytime net photosynthesis [eqns (47)], 24 h respiration to daytime gross photosynthesis [eqns (46)]	
S	Senescence rate [eqns (15), Fig. 1]	kg structural C m^{-2} d^{-1}
U	Utilization rate of substrate [eqns (12), Fig. 1]	kg substrate C m^{-2} d^{-1}
μ, μ_S, μ_X; μ(eg)	Proportional rates of growth [eqns (20)]; in exponential growth [eqns (25), (27)]	d^{-1}
π_g, π_g(eg); $\pi_{g,day}$, $\pi_{n,day}$	Specific gross photosynthetic rate [eqn (6)], in exponential growth [eqn (33)]; daily gross, net values [eqns (48)]	kg C (kg total C)$^{-1}$ d^{-1}
ρ, ρ_m, ρ_{night}, ρ_{24h}	Specific respiration rate [eqn (14)], at maintenance [eqns (31) or (42)], night value [eqns (48)], 24 h value [eqns (48)]	kg C respired (kg total C)$^{-1}$ d^{-1}

factor 86 400 s d^{-1} converts per second units to per day; 12/44 converts mass of CO$_2$ to mass of C. The light flux density I_0 of 50 here is for continuous light (giving a daily light receipt of 4·32 MJ photosynthetically active radiation (PAR) m^{-2} d^{-1} or 19·9 mol PAR m^{-2} d^{-1}); elsewhere a value of 100 is applied for a 12 h day, giving the same daily light receipt.

Equation (4) is used because of its simplicity and tractability. There are other better approaches available (e.g. Thornley and France, 2007, pp. 288–301; Johnson *et al.*, 2010). Although plant growth does of course depend on the parameters in eqn (4), the key results of our analysis are independent of the parameters in eqn (4) and its precise form, as long

as the equation applied to calculate gross photosynthetic rate can be linearized for low values of L_{AI} so that exponential growth is a possible solution.

It will be useful later when points of inflexion are calculated to have an expression of the differential of P_g with respect to M_{CX}, namely

$$\frac{dP_g}{dM_{CX}} = \frac{12}{44} 86400 \frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}} L_{AR} \exp(-L_{AR} M_{CX}) \quad (5)$$

This decreases exponentially with M_{CX} from 0·29 kg substrate C (kg structural C)$^{-1}$ d^{-1} when M_{CX} is small ($I_0 = 50$) at time $t = 0$ (Table 1a) towards zero as structural mass M_{CX} (and L_{AI}) $\to \infty$.

The specific instantaneous gross photosynthetic rate, π_g [kg C (kg total C)$^{-1}$ d^{-1}], is

$$\pi_g = \frac{P_g}{M_C} = \frac{P_g}{M_{CX} + M_{CS}} = \frac{P_g}{M_{CX}} \frac{1}{1 + C_S} \quad (6)$$

Total mass M_C is given in eqns (18); see eqn (11) for substrate fraction C_S. Note that increasing C_S decreases the specific gross photosynthetic rate.

At low and high values of light flux density I_0, eqn (4) approximates to

$$\left.\begin{array}{l} P_g(I_0 \to 0) = \frac{12}{44} 86400\ \alpha I_0 [1 - \exp(-L_{AI})] \\[2mm] P_g(I_0 \to \infty) = \frac{12}{44} 86400\ P_{max}[1 - \exp(-L_{AI})] \end{array}\right\} \quad (7)$$

For low values of leaf area index, L_{AI} [or structural mass, M_{CX}, eqn (3)], we write [from eqn (4)]

$$\left.\begin{array}{l} P_g = \frac{12}{44} 86400\ \frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}} L_{AR} M_{CX} = \beta M_{CX} \\[2mm] \beta(I_0) = \frac{12}{44} 86400\ \frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}} L_{AR} \end{array}\right\} \quad (8)$$

Parameter β has units of per day. In carbon units, it is the fraction of current structural C added per unit time via gross photosynthesis to the C substrate pool. It is a rectangular hyperbolic function of light flux density I_0. Values in the dark ($I_0 = 0$), at $I_0 = 50$ J PAR m^{-2} s^{-1} and its maximum are

$$\left.\begin{array}{l} \beta(I_0 = 0) = 0 \\[1mm] \beta(I_0 = 50) = 0·29 \\[1mm] \beta_{max} = \beta(I_0 \to \infty) = 86400\ \frac{12}{44} P_{max} L_{AR} = 0·589\ \text{d}^{-1} \end{array}\right\} \quad (9)$$

At high continuous light and low L_{AI}, gross photosynthesis adds C equal to approx. 60 % of the current structural C to the substrate C pool per day.

The linear expression $P_g = \beta M_{CX}$ of eqn (8) is valuable because it means that at low values of L_{AI} the plant grows

exponentially at a proportional growth rate dependent on I_0. Later, we use the inverse of the second of eqns (8), namely

$$\begin{array}{ll} I_0 = \dfrac{P_{max}}{\alpha} \dfrac{\beta}{\left(86400 \dfrac{12}{44} L_{AR} P_{max} - \beta\right)} & (10) \\[4mm] \quad = 50\ \dfrac{\beta}{\beta_{max} - \beta} = 50\ \dfrac{\beta}{0·589 - \beta} \end{array}$$

to calculate light flux density I_0 from a given value of β. Decreasing β decreases I_0.

Substrate utilization, U, respiration, R, and structural growth, G_X

Substrate 'concentration' or fraction, C_S [(kg substrate C) (kg structural C)$^{-1}$], is a useful intensive variable, defined as

$$C_S = M_{CS}/M_{CX} \quad (11)$$

Assuming that the volume of the reaction in which substrate utilization takes place is proportional to the mass of structural C, M_{CX}, then the rate of substrate C utilization, U (kg substrate C m^{-2} d^{-1}), is (assuming linear or mass-action kinetics with rate constant, k_S)

$$U = k_S M_{CX} C_S = k_S M_{CS}.\quad k_S = 1\ \text{d}^{-1} \quad (12)$$

With all defaults and in continuous light (Table 1b), this k_S value gives a substrate fraction C_S [eqn (11)] $= 0·27$ during the initial exponential growth phase [eqn (25)], and $C_S = 0·053$ at the steady state [eqn (42)]. A total of 63 % of an initial quantity of substrate is utilized within one 24 h day [$\exp(-k_S) = 0·37$] [eqn (12)].

Utilized flux of substrate C, U, is divided between structural growth, G_X, and respiration, R (kg C m^{-2} d^{-1}) (Fig. 1) [note: we are not now using McCree's units for R; see eqn (1)]:

$$\begin{array}{ll} G_X = Y_G U = Y_G k_S M_{CS}\ \text{and}\ R = (1 - Y_G)U & (13) \\[1mm] \quad = (1 - Y_G) k_S M_{CS}.\quad Y_G = 0·75 \end{array}$$

Y_G is a fraction ($0 \le Y_G \le 1$) termed growth efficiency or growth yield. Y_G values can vary considerably. The value of $Y_G = 0·75$ is fairly typical for vegetative plant material (e.g. Thornley and Cannell, 2000; Thornley and Johnson, 2000, pp. 350–353). No respiratory flux is associated with the senescence processes in Fig. 1. Such fluxes may exist and could be linked to outputs from a litter pool or to the inputs to that pool; they are omitted so that we retain the simplicity of a single respiratory output flux.

The instantaneous specific respiration rate, ρ [kg C respired (kg total C mass)$^{-1}$ d^{-1}], is [cf. eqn (6)]

$$\rho = \frac{R}{M_C} = \frac{(1 - Y_G) k_S M_{CS}}{M_{CS} + M_{CX}} = \frac{(1 - Y_G) k_S C_S}{1 + C_S} \quad (14)$$

For total mass M_C see eqns (18). ρ increases from zero to a maximum of $(1 - Y_G)k_S$ as C_S increases from zero to ∞.

Senescence flux S, *fluxes to litter,* I$_{lit}$, *and recycling of substrate,* I$_{rec}$

The proportional rate at which structure senesces is k_X (d^{-1}), giving a senescence flux of S (kg structural C m^{-2} d^{-1}, Fig. 1) of

$$S = k_X M_{CX}. \quad k_X = 0.04 \ d^{-1} \tag{15}$$

The fraction senescing or degrading per day is 4 %, giving a tissue lifetime of 25 d. No distinction is made between senescence and (non-pathological) degradation, and henceforth the process is referred to as senescence. More detailed plant models may distinguish between ageing and senescence, and non-age-related tissue turnover or degradation (e.g. Thornley, 1998). No respiratory flux is associated with senescence (see above). The structural C flux from senescence is divided between a fraction, f_{rec}, which is recycled to the substrate C pool with flux, I_{rec}, and the remainder, I_{lit}, which is input to a litter pool (Fig. 1). Thus

$$I_{rec} = f_{rec}S = f_{rec}k_X M_{CX} \text{ and } I_{lit} = (1 - f_{rec})S$$
$$= (1 - f_{rec})k_X M_{CX}. \quad f_{rec} = 0.5 \tag{16}$$

It is assumed that a constant 50 % of the senescing C is recycled. In general, it may be expected that this is a variable fraction depending on nutrient status (level of substrate fraction C_S) and tissue composition. Note that $0 < f_{rec} < 1$. In a real varying environment where substrate supply moves between scarce and plentiful, it does not seem unreasonable to take $f_{rec} = 0.5$ as representing an average value.

Differential equations

By inspection of Fig. 1 and using eqns (4), (12), (13), (15) and (16), these are

$$\left.\begin{array}{l} \dfrac{dM_{CS}}{dt} = P_g(M_{CX}) - k_S M_{CS} + f_{rec}k_X M_{CX}, \\[2mm] M_{CS}(t = 0) = 0.000005 \text{ kg substrate C } m^{-2} \\[2mm] \dfrac{dM_{CX}}{dt} = Y_G k_S M_{CS} - k_X M_{CX}, \\[2mm] M_{CS}(t = 0) = 0.0001 \text{ kg structural C} \end{array}\right\} \tag{17}$$

Gross photosynthetic rate P_g is written as P_g (M_{CX}) to emphasize that P_g is a function of state variable M_{CX} [Fig. 1, eqns (4), (3)]. The $t = 0$ value of substrate fraction C_S is 5 % [eqn (11)], defining $M_{CS}(t = 0)$ in terms of $M_{CX}(t = 0)$]. Denote total mass by M_C (kg C m^{-2}) and its rate of change by dM_C/dt

(kg C m^{-2} d^{-1}); therefore,

$$M_C = M_{CS} + M_{CX}$$
$$\frac{dM_C}{dt} = \frac{dM_{CS}}{dt} + \frac{dM_{CX}}{dt} = P_g(M_{CX}) - k_S M_{CS} + f_{rec}k_X M_{CX}$$
$$+ Y_G k_S M_{CS} - k_X M_{CX}$$
$$\frac{dM_C}{dt} = P_g(M_{CX}) - k_S(1 - Y_G)M_{CS} - k_X(1 - f_{rec})M_{CX}$$
$$\frac{dM_C}{dt} = P_g(M_{CX}) - R - I_{lit} = P_n - I_{lit}, \text{ where } P_n = P_g - R \tag{18}$$

Equations (13) and (16) have been applied. Net photosynthetic rate, P_n, is defined as gross photosynthesis P_g [eqn (4)] less respiration R [eqns (13)]. These two alternative forms for net photosynthesis, namely

$$P_n = P_g - R = \frac{dM_C}{dt} + I_{lit} \tag{19}$$

are used to check model formulation (stoichiometric validity) and programming.

Proportional growth rates of state variables (μ_S, μ_X) and total mass (μ)(d^{-1}) are

$$\left.\begin{array}{l} \mu_S = \dfrac{1}{M_{CS}} \dfrac{dM_{CS}}{dt} \\[3mm] \mu_X = \dfrac{1}{M_{CX}} \dfrac{dM_{CX}}{dt} \\[3mm] \mu = \dfrac{1}{M_C} \dfrac{dM_C}{dt} \end{array}\right\} \tag{20}$$

These are intensive variables which are constant during exponential growth.

The instantaneous ratio (r) of respiration R [eqns (13)] to gross photosynthesis P_g [eqn (4)], $r_{R:P_g}$, is

$$r_{R:P_g} = \frac{R}{P_g} \tag{21}$$

The equation for the double differential of total system C is [differentiating the third of eqns (18)]

$$\frac{d^2 M_C}{dt^2} = \frac{dP_g}{dM_{CX}} \frac{dM_{CX}}{dt} - (1 - Y_G)k_S \frac{dM_{CS}}{dt}$$
$$- (1 - f_{rec})k_X \frac{dM_{CX}}{dt} \tag{22}$$

With eqns (17) and (5), $d^2 M_C/dt^2$ can be written in terms of the state variables. Hence time of inflexion when $d^2 M_C/dt^2 = 0$ and state variable values at inflexion can be extracted numerically.

The differential eqns (17) could be non-dimensionalized [using eqn (4)], but not uniquely. This was not seen as a helpful simplification.

Exponential growth (eg)

There are two limiting cases for which analytical solutions exist. These are first exponential growth and secondly the steady state in a constant environment. In this section we examine exponential growth (eg). Exponential growth occurs at low L_{AI} [eqn (8)] when eqns (17) become

$$\left.\begin{array}{l} \dfrac{\mathrm{d}M_{CS}}{\mathrm{d}t} = \beta(I_0)M_{CX} - k_S M_{CS} + f_{rec}k_X M_{CX} \\[2mm] \dfrac{\mathrm{d}M_{CX}}{\mathrm{d}t} = Y_G k_S M_{CS} - k_X M_{CX} \end{array}\right\} \quad (23)$$

$\beta(I_0)$ is so written to make explicit that β is a function of light flux density I_0 [eqns (8)]. Assuming constant and equal proportional growth rates μ for M_{CS} and M_{CX} [eqns (20)] and constant substrate C fraction, C_S [eqn (11)], eqns (23) become (divide through by M_{CX})

$$\begin{array}{c} \mu C_S = \beta(I_0) + k_X f_{rec} - k_S C_S \\[2mm] \mu = Y_G k_S C_S - k_X \end{array} \quad (24)$$

These equations are solved for μ and C_S. Eliminating μ (the positive square root gives the biologically meaningful result)

$$\left.\begin{array}{l} Y_G k_S\, C_S^2 + (k_S - k_X)C_S - [\beta(I_0) + k_X f_{rec}] = 0 \\[1mm] a = Y_G k_S,\;\; b = (k_S - k_X),\;\; c = -[\beta(I_0) + k_X f_{rec}] \\[1mm] C_S(eg) = \dfrac{1}{2a}\left(-b + \sqrt{b^2 - 4ac}\right) \\[1mm] \mu(eg) = Y_G k_S C_S(eg) - k_X \end{array}\right\} \quad (25)$$

Here, 'eg' denotes exponential growth.

Plotting exponential growth rate $\mu(eg)$ against substrate fraction $C_S(eg)$ gives a straight line [last of eqns (25)], with zero growth occurring when

$$Y_G k_S C_S(eg; \mu = 0) = k_X;\; C_S(eg; \mu = 0) = k_X/Y_G k_S$$
$$= 0.05333^* \quad (26)$$

There is a minimum (non-zero) substrate fraction of 0.05333^* kg substrate C (kg structural C)$^{-1}$ (default parameters, Table 1b) below which the plant dies [$\mu(eg) < 0$]. Low values of the senescence rate constant k_X and high values of growth efficiency Y_G and substrate utilization rate constant k_S lead to a low value of $C_S(eg; \mu = 0)$ [see eqn (30) below].

In terms of the underlying parameters, $C_S(eg)$ and $\mu(eg)$ become [eqns (25)]

$$\left.\begin{array}{l} C_S(eg) = \dfrac{1}{2Y_G k_S} \\[1mm] \left(\sqrt{(k_S - k_X)^2 + 4Y_G k_S[\beta(I_0) + k_X f_{rec}]} - (k_S - k_X)\right) \\[2mm] \mu(eg) = \dfrac{1}{2} \\[1mm] \left(\sqrt{(k_S - k_X)^2 + 4Y_G k_S[\beta(I_0) + k_X f_{rec}]} - (k_S + k_X)\right) \end{array}\right\} \quad (27)$$

For small values of $\beta(I_0)$ [which is proportional to light flux density, I_0, eqn (8)], these are linearly proportional to β and

thence I_0 [because $\sqrt{(1 + x)} \approx 1 + \frac{1}{2}x$ for small x]. For large β, $C_S(eg)$ and $\mu(eg) \approx \sqrt{\beta}$. Remember that β has an asymptotic hyperbolic dependence on light flux density I_0, with asymptote β_{max} depending on maximum photosynthetic rate P_{max} [eqns (8), (9)].

In the dark ($I_0 = 0$), $\beta = 0$ [eqns (8)], eqns (27) become

$$\left.\begin{array}{l} C_S(eg; I_0 = 0) = \dfrac{1}{2Y_G k_S} \\[1mm] \left(\sqrt{(k_S - k_X)^2 + 4Y_G k_S k_X f_{rec}} - (k_S - k_X)\right) \\[1mm] = 0.0205\ \text{kg C substrate (kg structural C)}^{-1} \quad (28) \\[2mm] \mu(eg; I_0 = 0) = \dfrac{1}{2}\left(\sqrt{(k_S - k_X)^2 + 4Y_G k_S k_X f_{rec}} - (k_S + k_X)\right) \\[1mm] = -0.0246\,\mathrm{d}^{-1} \end{array}\right\}$$

Assuming that $k_S \gg k_X$ (Table 1b), these can be approximated by

$$C_s(eg; I_0 = 0; k_s \gg k_x) \approx f_{rec}k_x = 0.02\ \text{kg C substrate}$$
$$(\text{kg structural C})^{-1}$$

$$\mu(eg; I_0 = 0; k_s \gg k_x) \approx k_x(1 - f_{rec}Y_G) = -0.025\,\mathrm{d}^{-1}$$
$$(29)$$

The rate of decline in the dark is least if growth yield Y_G and recycling fraction f_{rec} are high (approaching unity).

The plant dies if $\mu < 0$. For β the second of eqns (27) gives an upper limit, and then eqns (10) and (9) give an upper limit of light flux density I_0, so that $\mu < 0$ implies

$$(k_S - k_X)^2 + 4Y_G k_S[\beta + k_X f_{rec}] \le (k_S + k_X)^2$$

$$\beta \le \dfrac{k_X(1 - Y_G f_{rec})}{Y_G} = 0.03333$$

$$I_0 \le \dfrac{P_{max}}{\alpha}\,50\,\dfrac{\beta}{\beta_{max} - \beta} = 50\,\dfrac{0.03333}{\beta_{max}(= 0.589) - 0.03333}$$

$$= 3\ \text{J PAR m}^{-2}\text{s}^{-1}[14 \times 10^{-6}\text{mol PAR m}^{-2}\text{s}^{-1}]$$

$$(30)$$

[This result can be derived directly from eqns (24) (eliminate C_S; write down the condition for $\mu < 0$).] Death of the plant depends on light flux density I_0 [eqn (8)], but the critical values of β and I_0 for positive growth are less (giving shade tolerance) for lower values of senescence rate parameter k_X, and for higher values of growth yield Y_G and recycling fraction f_{rec}. There is no dependence on substrate utilization rate constant k_S [eqn (12)].

At zero growth rate, the plant is just maintaining its *status quo*. The specific maintenance respiration rate [eqn (14)],

ρ_m, is [with eqn (26)]

$$
\left.\begin{aligned}
\rho(\text{eg}; \mu = 0) &= \rho_m = \frac{R}{M_C} = (1 - Y_G)\frac{k_S k_X}{Y_G k_S + k_X} \\
&= 0{\cdot}0127\,\text{d}^{-1} \\
\text{or for } k_S \gg k_X, \rho(\text{eg}; \mu = 0) &= \rho_m \approx \frac{1 - Y_G}{Y_G}k_X \\
&= 0{\cdot}0133^*\,\text{d}^{-1}
\end{aligned}\right\} \quad (31)
$$

Values for default parameters (Table 1b) are given. There is weak dependence on utilization rate k_S [eqns (12)] as generally $Y_G k_S \gg k_X$. ρ_m does not depend on recycling fraction f_{rec} (Fig. 1) [but see Fig. 4B and eqns (56) – the intercept of McCree's equation does depend on the recycling fraction f_{rec}].

The specific respiration rate for a plant in exponential decline in the dark is [eqns (14), (28)]

$$
\begin{aligned}
\rho(\text{eg}; I_0 = 0) &= \frac{R}{M_C} = \frac{(1 - Y_G)k_S C_S(\text{eg}; I_0 = 0)}{1 + C_S(\text{eg}; I_0 = 0)} \\
&= 0{\cdot}00502\,\text{d}^{-1}
\end{aligned} \quad (32)
$$

For $k_S \gg k_X$, this is approximately $(1 - Y_G)f_{rec}k_X = 0{\cdot}005$ d^{-1} [use eqns (29)]. This quantity is sometimes assumed to be a measure of the MR rate, but it is substantially less than the specific respiration rate required to maintain the plant's *status quo* [eqns (31)].

The specific gross photosynthetic rate, π_g [eqns (6), (8), (13)], for exponential growth, is

$$
\pi_g(\text{eg}) = \frac{\beta(I_0)}{1 + C_S(\text{eg})} \quad (33)
$$

For a given light level and value of β [eqn (8)], π_g decreases as the sugar level in the plant [$C_S(\text{eg})$, eqn (27)] increases (due perhaps to a decreasing k_S; Fig. 1, eqns (12)].

The ratio of respiration to gross photosynthesis (19) is [eqns (13), (8), then (27)]

$$
\begin{aligned}
r_{R:P_g}(\text{eg}) &= \frac{R}{P_g}(\text{eg}) = \frac{(1 - Y_G)k_S M_{CS}}{\beta M_{CX}} = \frac{(1 - Y_G)k_S C_S(\text{eg})}{\beta} \\
&= \frac{(1 - Y_G)}{2Y_G\beta}\left(\sqrt{(k_S - k_X)^2 + 4Y_G k_S(\beta + k_X f_{rec})} - (k_S - k_X)\right) \\
&= 0{\cdot}23
\end{aligned} \quad (34)
$$

The numerical value given is for $I_0 = 50$ W (PAR) m^{-2} (230 μmol PAR m^{-2} s^{-1}) giving β [eqn (8)] = 0·2945 d^{-1}. At zero growth rate this becomes

$$
r_{R:P_g}(\text{eg}; \mu = 0) = \frac{1 - Y_G}{1 - Y_G f_{rec}} = 0{\cdot}4 \quad (35)
$$

Here we used the second of eqns (30) with the equality to substitute for β and eqn (26) for C_S in the first line of eqns (34). The ratio at zero growth rate (maintenance) is 0·4 with default parameters (Table 1b) or 0·25 with no recycling ($f_{rec} = 0$) [see paragraph after eqns (16); also eqns (30) and following paragraph].

Steady state (ss)

In eqns (17), put the derivatives equal to zero, giving (ss denotes the steady state)

$$
\begin{aligned}
0 &= P_g(\text{ss}) - k_S M_{CS}(\text{ss}) + f_{rec}k_X M_{CX}(\text{ss}) \\
0 &= Y_G k_S M_{CS}(\text{ss}) - k_X M_{CX}(\text{ss})
\end{aligned} \quad (36)
$$

Solving for M_{CS}, M_{CX} and adding to give total mass M_C, therefore

$$
\left.\begin{aligned}
M_{CS}(\text{ss}) &= \frac{P_g(\text{ss})}{k_S(1 - f_{rec}Y_G)}, M_{CX}(\text{ss}) = \frac{Y_G P_g(\text{ss})}{k_X(1 - f_{rec}Y_G)} \\
M_C(\text{ss}) &= M_{CS}(\text{ss}) + M_{CX}(\text{ss}) = \frac{(k_X + k_S Y_G)P_g(\text{ss})}{k_S k_X(1 - f_{rec}Y_G)}
\end{aligned}\right\} \quad (37)
$$

To find the steady state, solve two equations for $P_g(\text{ss})$ and $M_{CX}(\text{ss})$ [from eqn (4) and the second of (37)]:

$$
\left.\begin{aligned}
P_g(\text{ss}) &= \frac{12}{44}86400\big(1 - \exp\{-[L_{AR}M_{CX}(\text{ss})]\}\big)\frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}} \\
P_g(\text{ss}) &= \frac{k_X(1 - f_{rec}Y_G)}{Y_G}M_{CX}(\text{ss})
\end{aligned}\right\} \quad (38)
$$

Eliminating $P_g(\text{ss})$ gives

$$
\begin{aligned}
\frac{k_X(1 - f_{rec}Y_G)}{Y_G}M_{CX}(\text{ss}) &= \frac{12}{44}86400 \\
\big(1 - \exp\{-[L_{AR}M_{CX}(\text{ss})]\}\big)&\frac{\alpha I_0 P_{max}}{\alpha I_0 + P_{max}}
\end{aligned} \quad (39)
$$

This transcendental equation can be solved numerically for $M_{CX}(\text{ss})$, e.g. using the Newton–Raphson method (Thornley and France, 2007, pp. 830–831), noting that eqn (39) is easily differentiated with respect to $M_{CX}(\text{ss})$. There is a trivial solution at $M_{CX} = 0$. There is a non-zero solution only if, at small M_{CX}, the slope of the right side of eqn (39) is greater than that of the left side. Therefore, using eqn (8) ($P_g = \beta M_{CX}$),

$$
\beta > \frac{k_X(1 - f_{rec}Y_G)}{Y_G} = 0{\cdot}03333 \quad (40)
$$

This inequality is equivalent to eqn (30) for plant death during the exponential growth phase. With eqn (10), it is equivalent to $I_0(\mu > 0) > 3$ J (PAR) m^{-2} s^{-1} [14×10^{-6} mol (PAR) m^{-2} s^{-1}] for standard parameters (Table 1b) [cf. eqn (30) and following paragraph].

Given that eqn (40) is satisfied and a non-trivial steady-state solution to eqn (39) exists for $M_{CX}(\text{ss})$ and therefore also $P_g(\text{ss})$ with either of eqns (38), the respiration rate R in the steady state becomes [eqns (13) and (37)]

$$
R(\text{ss}) = k_S M_{CS}(\text{ss})(1 - Y_G) = \left(\frac{1 - Y_G}{1 - f_{rec}Y_G}\right)P_g(\text{ss}) \quad (41)
$$

Hence follow several important ratios for steady-state plant ecosystems [for $C_S(ss)$, use eqn (11) and the second of eqns (36)], with parameters from Table 1b:

$$C_S(ss) = \frac{M_{CS}(ss)}{M_{CX}(ss)} = \frac{k_X}{Y_G k_S} = 0{\cdot}05333$$
$$r_{R:P_g}(ss) = \frac{R}{P_g}(ss) = \frac{1 - Y_G}{1 - f_{rec} Y_G} = 0{\cdot}4 \left.\rule{0pt}{60pt}\right\} \quad (42)$$
$$\rho(ss) = \rho_m = \frac{R(ss)}{M_C(ss)} = \frac{k_S k_X (1 - Y_G)}{k_X + k_S Y_G} = 0{\cdot}0127 \text{ d}^{-1}$$

These are all independent of environment, here light flux density, in contrast to these quantities during exponential growth [eqns (27), (34)] where they depend on β and light flux density I_0 [eqn (8)] apart from the specific MR respiration rate, ρ_m [eqn (31)]. The last of eqns (42), for specific respiration rate in the steady state, is obtained from the first of eqns (41) and the last of eqns (37). This is identical to eqn (31) for the specific respiration rate of a plant growing exponentially at zero rate. This important general result provides a link between long-term ecosystem behaviour and short-term experimentation on young plants. The $R:P_g$ ratio in eqns (42) has a simple interpretation with the Fig. 1 model because the denominator, $1 - x$ (say), can be expanded as $1 + x + x^2 + x^3 \ldots$, giving successive cycles of substrate use and re-use.

Diurnal environment

Assume that light flux density I_0 [eqn (4)] is varied on a daily basis, with 12 h of light followed by 12 h of darkness. The analysis of the last two sections dealing with exponential growth and a steady state in a constant environment is no longer possible. However, this more realistic situation can be examined numerically, obtaining results that may be compared with measurements such as those by McCree (1970) as well as with our analytical results for continuous light.

Define fractional daylength, f_{dl}, by

$$f_{dl} = 12 \text{ h daylight } (24 \text{ h})^{-1} = 0{\cdot}5 \quad (43)$$

Light flux density I_0 applied in eqn (4) to calculate photosynthesis is adjusted by dividing by fractional daylength:

$$I_0 := I_0 / f_{dl} \quad (44)$$

The symbol ': = ' means the value is replaced by. This ensures that daily light receipt is the same and makes simulations of a constant light regime and a 12 h day more comparable.

A critical issue is how, for a diurnal environment, are 'daily gross photosynthesis' and 'daily respiration' defined. These quantities, denoted by $P_{g,day}$ (kg C m^{-2} d^{-1}) and respiration, R_{24h} (kg C m^{-2} d^{-1}), are calculated with [eqns (4), (13)]

$$P_{g,day} = \int_0^{0{\cdot}5} P_g dt = \int_0^1 P_g dt, \quad R_{24h} = \int_0^1 R dt \quad (45)$$

Daylength is 12 h and light is applied from 0 to 12 h and darkness from 12 to 24 h. The ratio of 24 h respiration to daytime gross photosynthesis is

$$r_{R_{24h}:P_{g,day}} = \frac{R_{24h}}{P_{g,day}} \quad (46)$$

These quantities are calculated so that a comparison (albeit imperfect) with McCree's (1970) results can be made.

CO_2 gas exchange measurements generally give directly net photosynthesis during the day and respiration during the night. Again for comparison, and using an obvious notation, eqns (45) and (46) can be extended (including the fraction of 24 h respiration occurring during the night) [eqns (19), (13)]

$$P_{n,day} = \int_0^{0{\cdot}5} P_n dt, \quad R_{night} = \int_{0{\cdot}5}^1 R dt,$$
$$r_{Rnight:Pn,day} = \frac{R_{night}}{P_{n,day}}, \quad f_{Rnight:R24h} = \frac{R_{night}}{R_{24h}} \left.\rule{0pt}{50pt}\right\} \quad (47)$$

Specific values of daily photosynthesis and respiration are calculated by dividing by total mass M_C [eqns (18)] at the end of each 24 h day:

$$\pi_{n,day} = \frac{P_{n,day}}{M_C}, \quad \pi_{g,day} = \frac{P_{g,day}}{M_C}$$
$$\rho_{night} = \frac{R_{night}}{M_C}, \quad \rho_{24h} = \frac{R_{24h}}{M_C} \left.\rule{0pt}{45pt}\right\} \quad (48)$$

An exponential growth phase still occurs, now on a daily (24 h) basis rather than an instantaneous basis; there are fluctuations in proportional growth rates during the day [eqns (20)]. The steady state becomes a 24 h equilibrium state with diurnal variation.

Re-parameterization of the model

A more traditional single-state variable plant growth equation [cf. eqns (17) with two state variables] is obtained by making a zero-pool approximation (Thornley and France, 2007) and by eliminating one parameter in favour of a synthetic (emergent) McCree-type parameter.

Specific MR rate, ρ_m (d^{-1}), is [eqns (31) or (42)]

$$\rho_m = \rho(eg; \mu = 0) = \rho(ss) = \frac{k_S k_X (1 - Y_G)}{Y_G k_S + k_X} \quad (49)$$

Any of the three parameters: k_S, k_X or Y_G (Fig. 1) can be eliminated from the model in favour of ρ_m. We eliminate k_X, writing

$$k_X = \frac{\rho_m Y_G k_S}{(1 - Y_G) k_S - \rho_m} \quad (50)$$

The differential eqns (17) become

$$\frac{dM_{CS}}{dt} = P_g(M_{CX}) - k_S M_{CS} + f_{rec} \frac{\rho_m Y_G k_S}{(1 - Y_G) k_S - \rho_m} M_{CX}$$
$$\frac{dM_{CX}}{dt} = Y_G k_S M_{CS} - \frac{\rho_m Y_G k_S}{(1 - Y_G) k_S - \rho_m} M_{CX} \left.\rule{0pt}{55pt}\right\}$$
$$\quad (51)$$

For large values of k_S, substrate content M_{CS} is small, and is treated as a 'zero pool' so that inputs = outputs, $dM_{CS}/dt \sim 0$. Also assuming that $(1 - Y_G)k_S \gg \rho_m$ [eqns (13), (12), (31), (42)], the first equation becomes

$$0 = P_g(M_{CX}) - k_S M_{CS} + f_{rec}\frac{\rho_m Y_G}{(1 - Y_G)}M_{CX} \qquad (52)$$

Substituting for $k_S M_{CS}$ from eqn (52) in the second of eqns (51), and again for large k_S [eqn (49) is used for the specific MR rate, ρ_m]:

$$\frac{dM_{CX}}{dt} = Y_G\left(P_g(M_{CX}) + f_{rec}\frac{\rho_m Y_G}{(1 - Y_G)}M_{CX}\right) - \frac{\rho_m Y_G}{1 - Y_G}M_{CX}$$

$$\frac{dM_{CX}}{dt} = Y_G P_g(M_{CX}) - (1 - Y_G f_{rec})\frac{\rho_m Y_G}{1 - Y_G}M_{CX}$$

$$\frac{dM_{CX}}{dt} = Y_G\left(P_g(M_{CX}) - \rho_m\frac{1 - Y_G f_{rec}}{1 - Y_G}M_{CX}\right) \qquad (53)$$

Finally

$$\left.\begin{array}{l}\dfrac{dM_{CX}}{dt} = Y_G P_g(M_{CX}) - mM_{CX}\\[2mm]m = \rho_m Y_G\dfrac{1 - Y_G f_{rec}}{1 - Y_G} = (1 - Y_G f_{rec})k_X\end{array}\right\} \qquad (54)$$

This is a single-state variable plant growth equation. The coefficient (for $k_S = 100\,d^{-1}$), m, is

$$m = 0.025\,d^{-1} \qquad (55)$$

This can be compared with the specific MR rate of $\rho_m = 0.0133*\,d^{-1}$ [eqn (31)]. It is mistaken to interpret m as the maintenance requirement. Integration of eqn (54) or of eqns (17) with $k_S = 100\,d^{-1}$ (say) gives exactly the same time course for M_{CX}, so long as respiration is still defined by eqns (13).

This result depends on the assumptions in Fig. 1. The crucial assumption concerns respiration rate R [here given by eqn (13) with $k_S M_{CS}$ now given by eqn (52) in the zero-pool approximation]; the rest is stoichiometry. Equation (13) is what Warren Wilson *et al.* (1986) call a 'conditional' equation which represents a scientific hypothesis. When C conservation (stoichiometry) is considered, many equations that are 'identities' can be written down which are algebraically self-evident [e.g. eqns (19)]. The terms 'conditional equations' and 'identities' are sometimes referred to as 'synthetic statements' and 'tautologies' (e.g. Ayer, 2001). Van Oijen *et al.*'s analysis (2010) consists mostly of identities, although two conditional equations are introduced: for respiration R ($R = MR + GR$), and then $MR = GR$.

Numerical methods

Programming was in ACSL (Advanced Continuous Simulation Language, Aegis Research, Huntsville, AL, USA; version 11·8·4), a fortran-based ordinary differential equation (ODE) solver. The ODEs are integrated using Euler's method with a fixed integration interval of $\Delta t = 1/128\,d$

(11·25 min). A program listing can be obtained from the author.

RESULTS AND DISCUSSION

Standard growth curve

With default parameters and a constant environment (Table 1b), plant mass grows as in Fig. 2A. This 'expo-asymptotic' curve has a period of almost constant exponential growth from time $t = 3$ d to 10 d when the L_{AI} reaches 0·02. After a maximum, growth rate rapidly declines. Asymptotic L_{AI} (not shown, but see Fig. 6A with $I_0 = 50$) is 8·8 (it is approx. 6 for a 12 h day). This was felt to be acceptable for a simple model simulating vegetative growth. In Fig. 2, the asymptote is at final mass $M_C = 0.1861$ which is 3·83 times the mass at the inflexion point. Logistic and Gompertz growth equations gives 2 and $2.7818 = e$ for this ratio (Thornley and France, 2007, p. 144, equation 5·19 and p. 147, equation 5·28).

In Fig. 2B the ratio of respiration R [eqns (13)] to gross photosynthesis P_g [eqns (4), (21)] is drawn. After an unimportant transient, it increases from a value during exponential growth of 0·23 [eqns (34)] to an asymptotic value of 0·4 [eqns (42)].
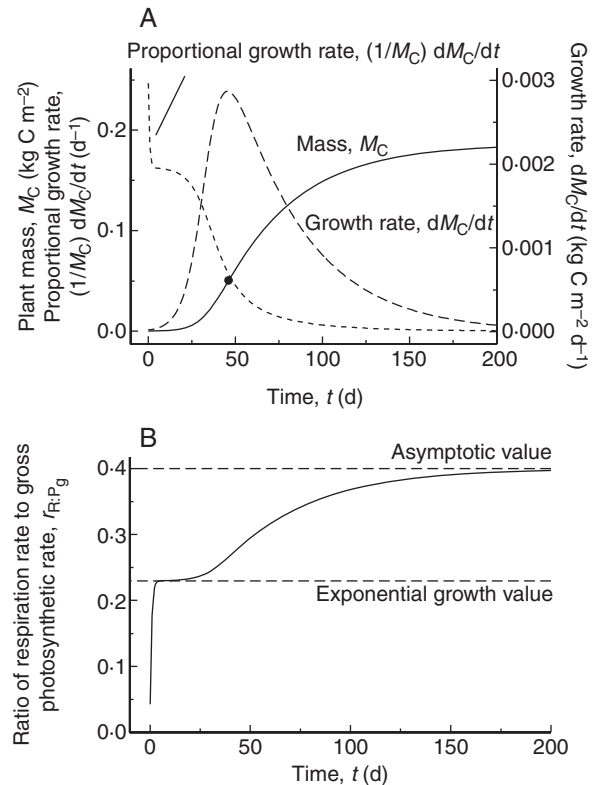

Fig. 2. Growth curve in a constant environment with default parameters (Table 1b). (A) Plant mass, M_C, eqn (18); growth rate, dM_C/dt, eqn (18); and proportional growth rate of total mass, $(1/M_C)\,dM_C/dt$, eqns (20). The black circle shows the inflexion point on the graph for M_C (continuous line). (B) Ratio of respiration R [eqns (13)] to gross photosynthesis P_g [eqns (4)], $r_{R:P_g}$ [eqn (21)]. The dashed lines show the value of the ratio during exponential growth (0·23) and at steady state (0·4) [eqns (34), (42)].

Exponential growth

The analysis for an exponentially growing plant in a constant light environment is given in eqns (23)–(35). This corresponds to the 3–10 d time period shown in Fig. 2. In Fig. 3, light flux density I_0, and thereby parameter β [eqn (8)], is varied across a range of I_0 from near zero to 500 J (PAR) m^{-2} s^{-1} (2300 µmol m^{-2} s^{-1}). Results are plotted against specific gross photosynthetic rate, π_g [eqns (6), (33)]. Two values for the substrate utilization constant k_S [Fig. 1; eqn (12)] are applied to demonstrate the effects of low and high substrate content (Fig. 3D).

In Fig. 3A, specific growth rate μ [eqns (20)] increases with specific gross photosynthetic rate π_g, but at an increasing rate (Fig. 3E). This is because the substrate fraction [C_S, eqns (11), (27)] increases with π_g (Fig. 3D) and there is no yield factor such as Y_G (Fig. 1) operating for the substrate component of dry matter. At low light (low π_g) and for high k_S, the substrate

fraction is low; nearly all growth is structural which incurs the Y_G penalty. The $k_S = 5$ d^{-1} line in Fig. 3E approaches $Y_G = 0.75$ at low light (low π_g).

Respiration is a decreasing fraction of increasing photosynthesis (Fig. 3B, C, F). The decrease in this fraction is marked for the $k_S = 1$ d^{-1} lines because the substrate fraction increases to high values (Fig. 3D). The specific respiration rate ρ [Fig. 3B, eqn (14)] when growth rate μ is zero [eqn (31)] has values of 0.0127 and 0.0132 d^{-1} for $k_S = 1$ and 5 d^{-1}.

Corresponding to the decreasing respiration fraction of Fig. 3B and F, the ratio of respiration to gross photosynthesis [eqn (21)] (Fig. 3C) decreases with increasing light. At zero growth rate this has a value of 0.4 [eqn (35)], decreasing for higher growth rates as the substrate fraction increases (Fig. 3D). The higher value of the substrate utilization constant $k_S = 5$ d^{-1} gives lower values of the substrate fraction (Fig. 3D). Plant substrate fractions can cover a wide range,
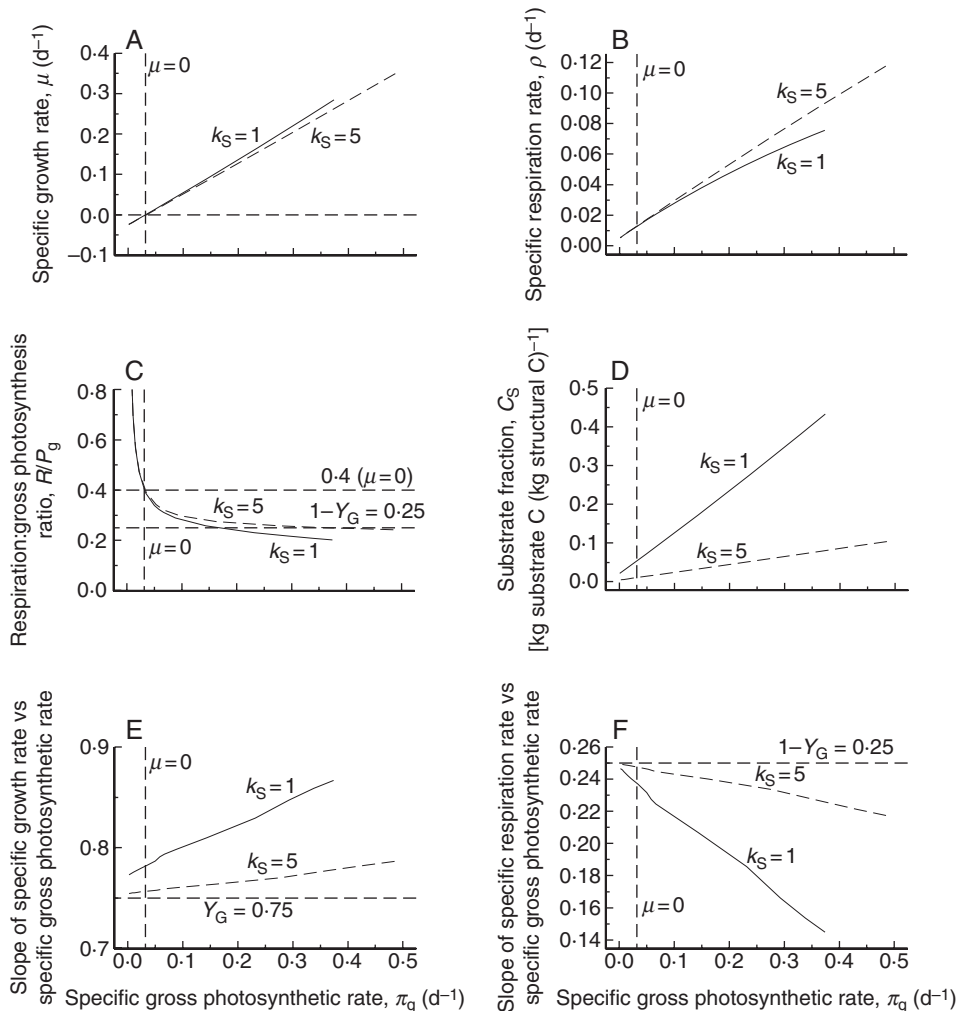

FIG. 3. Exponential growth solutions [eqns (23) to (35)] in constant conditions. Light flux density, I_0, and hence parameter β [eqn (8)], are varied from near zero to 500 J (PAR) m^{-2} s^{-1} (2300 µmol PAR m^{-2} s^{-1}). Two values of parameter k_S are applied. Specific gross photosynthetic rate π_g is given by eqn (33). The vertical dashed line labelled $\mu = 0$ marks the π_g value for zero specific growth rate, $\mu = 0$, for $k_S = 1$ d^{-1} (the value is slightly different for $k_S = 5$ d^{-1}) [eqns (33), (30), (27)]. (A) Specific growth rate μ, eqns (27); (B) specific respiration rate ρ, eqns (14), (27); (C) respiration:gross photosynthesis ratio $r_{R:P_g}$, eqns (21), (13), (8), (27); (D) substrate fraction C_S, eqn (27), (8); (E, F) slopes of graphs in (A) and (B), respectively, were calculated numerically.
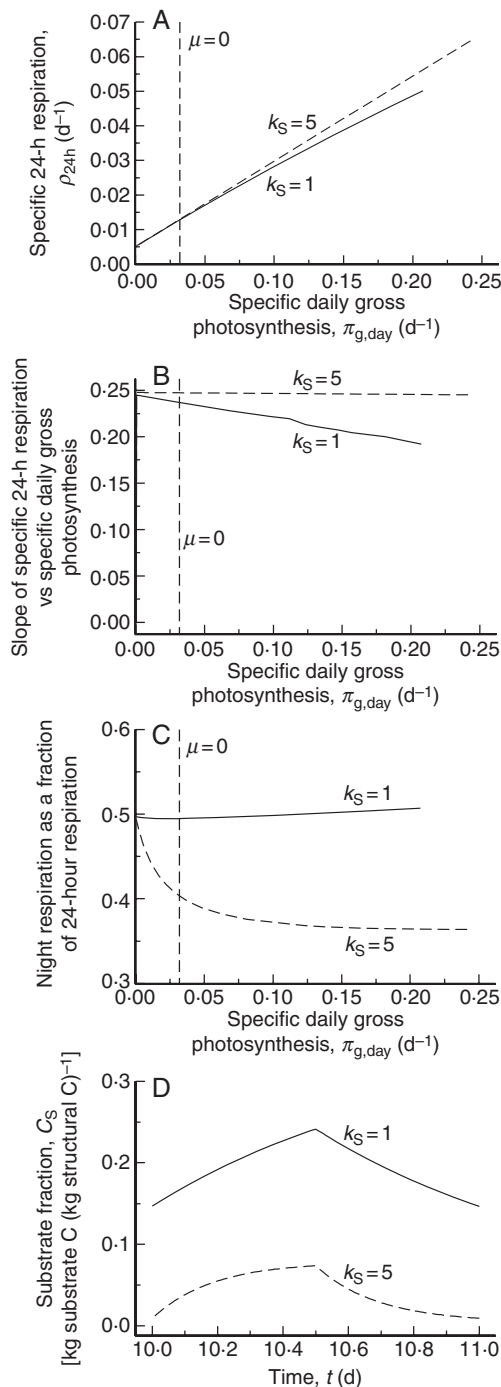
FIG. 4. Simulation of McCree's equation [eqn (2); McCree, 1970]. A 12-h day-length is applied followed by 12-h darkness. In (A), (B) and (C), light during the day was varied from a low value to 1000 J (PAR) m^{-2} s^{-1} (4600 μmol PAR m^{-2} s^{-1}). Two values of utilization rate constant k_S were applied, giving high and low substrate plants. Plants are in 24 h exponential growth, attained after 10 d from low initial values (Table 1a). (A) McCree's formulation [eqns (1), (2); McCree, 1970] is followed. (B) Slopes of the lines in (A) are calculated numerically. (C) The fraction of 24 h respiration occurring during the night is calculated assuming eqn (13) for respiration R is valid during the day and night [eqns (47)]. (D) Time courses of the substrate fraction are illustrated for a daytime light flux density of $I_0 = 100$ J (PAR) m^{-2} d^{-1} (460 μmol PAR m^{-2} d^{-1}). Specific 24-h respiration ρ_{24h} and specific daily gross photosynthesis $\pi_{g,day}$ are calculated in eqns (48). The vertical dashed lines labelled $\mu = 0$ in (A), (B) and (C) indicate where daily specific growth rate $\mu = 0$.

from a few per cent up to 20–30 %, depending on species, growing conditions and time of day and season.

McCree's experiment

Now we apply the model to McCree's (1970) equation [our eqn (1)], attempting to follow his experimental protocol closely. No parameter tuning was attempted and default parameters are used (Table 1b). In eqn (4), light flux density I_0 is applied at a constant level for 12 h between the hours of 0 and 12 h; otherwise between 12 h and 24 h, $I_0 = 0$. It is assumed that McCree's plants were approximately in exponential growth, and here the simulated plants are in 24 h exponential growth. This is obtained accurately enough at time $t = 10$ d by using the initial values ($t = 0$) of Table 1a, and lasts until the leaf L_{AI} is approx. 0.02, which depends on light flux density I_0. As in Fig. 3, two values of the substrate utilization rate constant k_S are applied (Fig. 1), so that the effects of high (with $k_S = 1$ d^{-1}) and low (with $k_S = 5$ d^{-1}) substrate fractions can be seen (Fig. 3D). Daily gross photosynthesis $P_{g,day}$ (kg C m^{-2} d^{-1}) and daily (24 h) respiration R_{24h} (kg C m^{-2} d^{-1}) are obtained with eqns (45). $P_{g,day}$ and R_{24h} are both divided by the plant mass, M_C [kg C m^{-2}, eqn (18)], at 24 h to give specific daily gross photosynthesis, $\pi_{g,day}$ (d^{-1}) and specific daily respiration, ρ_{24h} (d^{-1}) [eqns (48)]. It is assumed that respiration R continues according to eqn (13) during both day and night (but see below). A range of daytime light flux densities I_0 [eqns (8)] from near zero up to 1000 J (PAR) m^{-2} s^{-1} (4600 μmol PAR m^{-2} s^{-1}) gives a range of $\pi_{g,day}$. Low values of I_0 can give negative daily growth rates.

Figure 4A shows respiration vs. photosynthesis for two values of k_S. The lines are curvilinear, but assuming linearity both have an intercept of approx. 0.005 d^{-1}. When slopes are plotted as in Fig. 4B, the lack of linearity is more apparent, especially for the lower k_S value which gives higher substrate fractions (Fig. 4D). The curvilinearity is less at high k_S values where substrate fractions are smaller (Fig. 4D). Comparing Fig. 4A with McCree's equation in the form of eqn (2), our intercept of 0.005 d^{-1} of a curve may be compared with McCree's value of 0.015 d^{-1} from fitting a straight line to data (McCree, 1970, p. 227). Drawing a tangent to the $k_S = 1$ curve in Fig. 4A at higher values of abscissa will give substantially higher values of the intercept. For low substrate ($k_S = 5$ d^{-1}) the slope decreases from approx. 0.248 to 0.245 (Fig. 4B) as photosynthesis increases; for high substrate ($k_S = 1$ d^{-1}) the slope decreases from 0.25 to 0.19. This occurs because growth in substrates does not incur a respiration penalty as does growth in structure. These slopes can be compared with McCree's estimate of 0.25 (McCree, 1970, p. 227). As no parameter tuning has been applied, the general agreement with McCree's values is reasonable.

Assuming that respiration throughout the 24 h is given by eqns (45) and (13) (but see below), a fraction for night-time respiration [eqns (47)] can be calculated (R_{night}/R_{24h}). This is plotted in Fig. 4C. For the high substrate plants ($k_S = 1$ d^{-1}) this is roughly constant at about 0.5 (the small increase above 0.5 shown in Fig. 4C is due to the way in which the simulations were made: night follows day and the plants are larger (in structural terms) during the night due to growth and therefore respire slightly faster, although average substrate

levels at night are always lower than during the day [eqns (13) for *R*, Fig. 4D]. For low substrate plants ($k_S = 5$ d^{-1}), night respiration is well below the 0·5 expected from daylength alone, because for high k_S average substrate level at night is much less than during the day (Fig. 4D).

Sensitivity of McCree equation parameters to key model parameters

Now we use the method of the last section (examining 24 h exponential growth solutions) to investigate the sensitivity of McCree equation parameters [McCree, 1970, p. 227; our eqn (2)] to key model parameters. These are: growth yield, Y_G; recycled fraction, f_{rec}; senescence rate constant, k_X; utilization rate constant, k_S; and fractional daylength, f_{dl} (Fig. 1).

First from Fig. 4A and B, we note that McCree's linear equation [eqn (2)] is only approximately satisfied by the model's predictions, which are in general curvilinear. Therefore, exact equations relating McCree parameters k and c of eqn (2) to model parameters (Fig. 1; Table 1b) cannot be expected.

Growth yield Y_G (Fig. 5A) affects both slope and intercept [eqn (2), k, c] of specific 24 h respiration vs. specific daily photosynthesis [eqn (48)]. The recycling fraction f_{rec} (Fig. 5B) affects the intercept proportionately but not the slope. With $f_{rec} = 0$, the intercept is indeed zero. Senescence rate constant k_X (Fig. 5C) similarly affects the intercept (proportionately) but not the slope. The utilization rate constant k_S (Fig. 5D) has asymptotic effects on slope (see also Fig. 4A, B) and intercept (as $k_S \to \infty$ the lines superimpose). A k_S value of 50 d^{-1} gives a response that is little different from the $k_S = 1$ d^{-1} response. However, lower values of k_S (<1 d^{-1}) cause substrate fraction C_S to be high (Figs. 3D, 4D); no respiration is associated with growth of substrate so this decreases specific respiration at higher values of specific gross photosynthesis; responses become more convex and the slope and intercept are decreased. In Fig. 5E, fractional daylength (f_{dl}) is altered. Light flux density I_0 [eqn (4)] is adjusted so that the total daily light receipt is the same. i.e. light flux density I_0 is twice as large for $f_{dl} = 0.25$ (a 6 h day) as for $f_{dl} = 0.5$ (a 12 h day). Because of the non-linear nature of eqn (4), daily gross photosynthesis is less for $f_{dl} = 0.25$ than for $f_{dl} = 0.5$. Perhaps surprisingly, neither intercept nor slope is affected as daylength is altered. However if night-time respiration is plotted against daytime net photosynthesis [eqns (47)] then both slope and intercept are proportional to daylength [eqns (58)].

The results in Fig. 5 suggest that the two parameters of eqn (2) are given roughly by

$$k \approx (1 - Y_G), \quad c \approx k_X(1 - Y_G)f_{rec} \qquad (56)$$

Slope k depends only on yield constant Y_G (Fig. 5A). Y_G affects intercept c, which is also affected by senescence rate k_X and recycling fraction f_{rec} (Fig. 5B, C). In eqns (56) no dependence on the substrate utilization rate constant k_S is included, which is reasonable if $k_S = 1$ d^{-1} or higher.

Equations (56) suggest that McCree's k parameter [eqns (2)] can be interpreted directly in terms of growth efficiency Y_G. Perhaps more interesting is McCree's c parameter, often
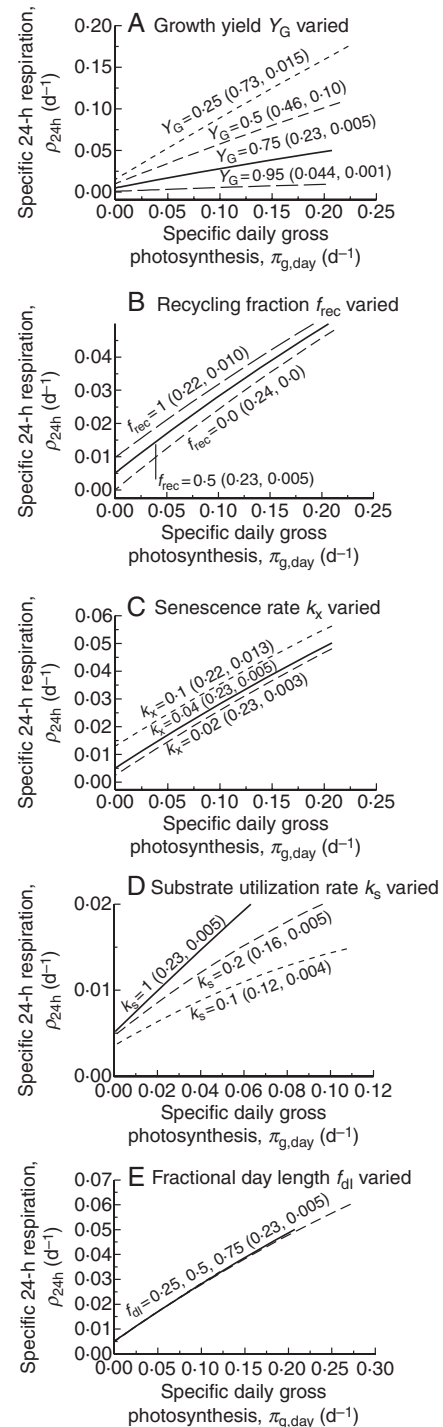

FIG. 5. Sensitivity of McCree equation plots [McCree, 1970, p. 227; our eqn (2)] to the principal parameters of the model (Fig. 1, Table 1b). A 12-h day-length is applied followed by 12-h darkness. Light during the day was varied from near zero to 1000 J (PAR) m^{-2} s^1 (4600 μmol PAR m^{-2} s^{-1}). Plants are in 24 h exponential growth, attained after a few days from low initial values (Table 1a). The continuous line is for the default parameter values (Table 1b). (A) Growth efficiency, Y_G; (B) recycled fraction, f_{rec}; (C) senescence rate constant, k_X; (D) substrate utilization rate constant, k_S; (E) fractional daylength, f_{dl}. In each case approximate corresponding values of the parameters of eqn (2) are given in brackets: (slope, k; intercept, c); (McCree, 1970, p. 227). Specific 24-h respiration ρ_{24h} and specific daily gross photosynthesis $\pi_{g,day}$ are calculated in eqns (48).

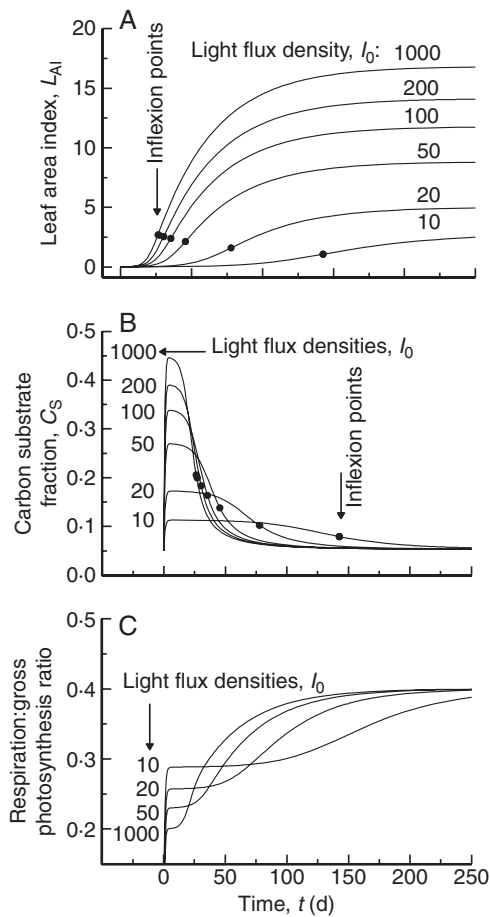FIG. 6. The model is run in constant light flux densities (daylength = 24 h) from near zero to 1000 J (PAR) m^{-2} s^1 (4600 µmol PAR m^{-2} s^{-1}) to a steady state with default parameter values (Table 1b). Instantaneous values are plotted at daily intervals. (A) Leaf area index, L_{AI} [eqns (3)] [black circles show inflexion points for total mass, eqns (18)]; (B) C substrate fraction, C_S [eqn (11)]; (C) ratio of respiration to gross photosynthetic rate, $r_{R:P_g}$ [eqns (21)].

Steady-state simulations

Short-term experiments (e.g. McCree, 1970) give valuable data, although interpretation may not be straightforward. However, the steady state of ecosystems is often of interest. Now we examine how the model parameters contribute to steady-state properties [eqns (36)–(42)]. First a true steady state when light flux density is constant is examined.

Figure 6A shows how asymptotic L_{AI} is increased by light flux density. Inflexion points are shown; the ratio of inflexion L_{AI} to asymptotic L_{AI} decreases from 0.39 at low light ($I_0 = 10$ W PAR m^{-2} = 46 µmol PAR m^{-2} s^{-1}) to 0.16 at high light ($I_0 = 1000$ W PAR m^{-2} = 4600 µmol PAR m^{-2} s^{-1}). At high light the growth curve becomes less 'logistic-like' (where the ratio is 0.5, e.g. Thornley and France, 2007, equation 5·19, p. 144).

Figure 6B illustrates how C substrate fraction C_S [eqn (11)] has a value which, during exponential growth, depends on light flux density [eqns(27)], but which then decreases asymptotically to a common value of 0.05333 [eqn (42)].

The ratio of respiration to gross photosynthesis [eqn (21)] is drawn in Fig. 6C. For young exponentially growing plants this is light dependent, with a low value at high light – decreasing light flux density increases this ratio [eqns (34)], until, at zero exponential growth rate, the ratio is 0.4 [eqn (35)]. In the steady state, a ratio of 0.4 [eqn (42)] is approached for all light flux densities even although the L_{AI} asymptotes are very different (Fig. 6A). This suggests that plant ecosystems not in the steady state can be expected to have differing ratios of respiration to gross photosynthesis, but in the steady state these tend to the same value [eqn (42)], which may be substantially independent of environment and ecosystem.

12-hour daylength simulations

If the system is driven by 12 h daylength (with daytime light levels doubled), the results are qualitatively as in Fig. 6 for a constant environment (now extracting and comparing daily averages or integrated fluxes). However, equilibrium L_{AI} valuess are about half of the value in continuous light (Fig. 6A). Substrate fractions are much lower (about half) than in Fig. 6B during exponential growth. Surprisingly, the steady state daily average substrate fraction for the diurnal situation is the same as the steady state value for the constant environment [Fig. 6B; eqns (42)]. The ratio of respiration to gross production as defined by eqn (46) ranges from approx. 0·25 (exponential growth, depending on light level) to 0·4 (steady state, for all light levels), showing the importance of growth conditions and position in the life cycle between exponential growth and the steady state for this ratio.

Respiration is zero during the daylight hours

Next we explored the consequences of assuming that, during the 12 h light period of the diurnal environment, growth efficiency Y_G is unity, instead of 0·75 [eqn (13)]. When illuminated, there is excess energy currency present allowing synthesis to occur without cost – there is no need to degrade photosynthetically fixed C to provide energy units for synthetic processes (Krömer, 1995). This assumption is made

viewed as a 'maintenance' coefficient. According to the second of eqns (56), it depends on growth efficiency Y_G, and is proportional to senescence rate k_X and fraction of senescing material recycled f_{rec} (Fig. 1). This differs from our extracted maintenance coefficient in eqns (31) and (42), which for high k_S depends only on k_X and Y_G.

If we re-write McCree's eqn (2) as

$$\rho_{night} = k'\pi_{n,day} + c' \qquad (57)$$

using specific night-time respiration and specific daily net photosynthesis as defined in eqns (48) (these are measured quantities), then a replot of Fig. 5 using these changed variables gives approximate parameters of

$$k' \approx (1 - f_{dl})(1 - Y_G), \quad c' \approx k_X(1 - f_{dl})(1 - Y_G)f_{rec} \qquad (58)$$

Now fractional daylength [f_{dl}, eqn (43)] plays an important role [cf. eqns (56)–(58)].

for all light levels applied. These simulations are qualitatively as in Fig. 6. Compared with the 12 h day simulations reported in the last section, L_{AIS} are higher; substrate fractions are slightly lower (due to the greater dilution from increased growth – in fact there are higher amounts of substrate, M_{CS}, Fig. 1). The ratio of 24 h respiration to daily gross photosynthesis [eqn (46)] is lower because daytime respiration is zero when $Y_G = 1$ [eqns (13)]. For the respiration to gross photosynthesis ratio, all curves approach the common asymptote of $r_{R24h:P_{gday}} = 0.22$ as compared with 0.4 in the last two sections (e.g. Fig. 6C). This simulation demonstrates that any direct coupling of photosynthetically produced energy to growth processes could have large effects on respiration.

Respiration in the dark

Placing a plant, or part of a plant, in the dark, sometimes for prolonged periods, is sometimes used to give an estimate of 'maintenance' respiration (Gary *et al.*, 2003). This topic has been partially addressed in the exponential growth section and eqns (28), (29) and (32). Here, in order to give some comparison with Gary *et al.* (2003, fig. 1), the plant is grown in low and high continuous light [$I_0 = 20$, 1000 J PAR m^{-2} s^{-1} (92, 4600 μmol PAR m^{-2} s^{-1}); Fig. 6] to a steady state, achieved by time $t = 1000$ d [eqns (42)]. Then the plant is placed in darkness and the time course of the specific respiration rate ρ, C substrate fraction C_S and plant mass M_C is examined [eqns (14), (11), (18)]. Results are shown in Fig. 7.

Plant mass is much higher at the higher light level, although the specific respiration rate $\rho(ss)$ and substrate fraction $C_S(ss)$ [eqns (42)] are independent of light level. After switching off the light (at time $t = 1000$ d), both these intensive quantities decline identically over some 10 d to their new constant values in the dark [eqns (32), (28)].

Comparison of Fig. 7 with fig. 1 of Gary *et al.* (2003), who plot tomato whole-plant respiration rate in prolonged darkness, shows that many extensions would be needed in order to simulate real data. Issues include: multiple substrates, multiple structural components with different growth/senescence/recycling characteristics, and possibly reaction switches in order to obtain increases in respiration rate.

CONCLUSIONS

The recycling model of Fig. 1 is able to account for three issues in plant respiration.

First, required for the model's credibility, is to give an account of McCree's equation [McCree, 1970; our eqns (1) and (2)], which is measurement based, and arguably is why many researchers follow GMRP. This is spelt out in Fig. 4A, where it is assumed that plants are in exponential growth. The simulations of Fig. 5 reveal how McCree's parameters can be approximated by parameters of the model (Fig. 1) as given in eqns (56). Indeed our analysis suggests that the MR rate is not directly related to McCree's c parameter [eqn (2)], but is better regarded as the specific respiration rate at zero growth rate [eqns (31), (42)]. If McCree's equation is modified so that it relates more directly to measured quantities as in eqn (57), then the modified parameters can be approximated by eqns (58), where daylength is now important.
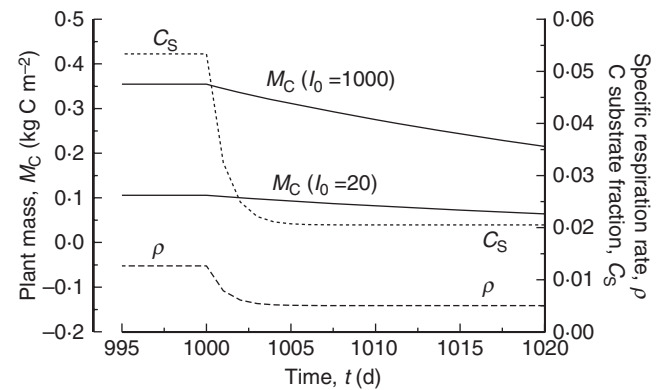

FIG. 7. Respiration decline in the dark. Plants are grown to a steady state [eqns (36)–(42)] at high and low continuous light [eqns (4)], $I_0 = 1000$, 20 J PAR m^{-2} s^{-1} (4600, 92 μmol PAR m^{-2} s^{-1}). At time $t = 1000$ d, light is switched off. Plant mass M_C is given in eqns (18), specific respiration rate ρ [kg C respired (kg total C)$^{-1}$ d^{-1}] by eqn (14), and substrate fraction C_S [kg substrate C (kg structural C)$^{-1}$] by eqn (11).

The second issue concerns the nature of MR, which has long been a controversial concept (Wohl and James, 1942). Many may doubt the existence of a separate process which could be dubbed 'maintenance'. It is difficult to represent an MR process in crop and ecosystem models directly and effectively – such efforts easily give rise to unacceptable behaviour or *ad hoc* assumptions being introduced into the model. The approach of Fig. 1 provides a mechanistic alternative, which it is straightforward to extend to deal with more detailed aspects of plants and crops.

The third and last issue concerns the ratio of respiration R to gross photosynthesis P_g [eqn (21)]. The topic has been addressed frequently over many years (e.g. Gifford, 2003) and recently by van Oijen *et al.* (2010). The model demonstrates that for a growing crop the ratio is expected to vary with time, as illustrated in Figs 2B and 6C. During exponential growth [eqns (34)], the ratio depends on light flux density, I_0 [via eqns (8)]. In equilibrium [e.g. a mature plant ecosystem, eqns (42); see also eqn (35)] the ratio is constant, depending only on two parameters, and is independent of environment. This is demonstrated by the common asymptotes in Fig. 6C where the ratio is 0.4 for all values of light flux density. The value of 0.4 is likely to be conservative as growth yield $Y_G = 0.75$ is a well-established value for plant ecosystems where cellulose or similar compounds are a major component, and, as mentioned after eqns (16), $f_{rec} = 0.5$ may be a reasonable guess at the average fraction of senescing material recycled for real variable environments (note that f_{rec} must lie between zero and unity).

Gifford (2003) remarked that 'Plant respiratory regulation is too complex for a mechanistic representation in current terrestrial productivity models for C accounting ...'. That may be true, but surely it is a council of despair – attempting to grasp and pin down complexity is often the first step to finding a way through the labyrinth. Many attempts have been made to understand in a simple manner the relationships between photosynthesis, growth, respiration and net production. These have not been successful, sometimes because they ignore some of the basic principles of reductionist

science and of explanatory dynamic simulation, promulgated by de Wit (1970) and others.

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